

Article

Key to marine arthropod larvae

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Abstract

The scope of this key is restricted to the larvae of marine arthropods. The key is based solely on their morphology, patterns of body segmentation, numbers of appendages, and mode of locomotion. An effort has been made to treat all traditionally named larval forms, both planktonic and benthic. It is intended that this key be useful for a researcher working with archived museum specimens and therefore, does not include habitat information as a identifying trait, even though this information is usually available in the archived records. Within the phylum Arthropoda there are two sub-phyla and eleven classes having larval stages in the marine environment. Where feasible the original names of the various larval types have been used. Because this nomenclature is less commonly used today compared to the past, the more recent taxonomic affinities are included in parentheses after the original larval name. The key includes the following thirty-four larvae: Branchhiopoda nauplii; Cephalocarida nauplii; Mystacocarida nauplii; trilobite larva; protonymphon; hexapod larvae; Remipedia nauplii; nauplius - Y larvae; Cirripedia nauplii; Ascothoracida nauplii; Ostracoda nauplii; Euphausiacea nauplii; Penaeidea nauplii; Cyclopoida nauplii; Calanoida nauplii; Harpacticoida nauplii; Polyarthra nauplii; cypris larva; eryonecius larva; cypris-Y larva; elaphocaris larvae; mysis larvae; lucifer zoea; acetes zoea; acanthosoma larva; phyllosoma; antizoea larva; anomuran zoea; brachyuran zoea; calyptopis larvae; furcilia larva; crytopia larva; puerulus larva; alima larva.

Keywords larvae; nauplii; zoea; megalopa; protonymphon; arthropoda.

1 Introduction

Various authors define the term larva differently. The differences result from different perspectives and or research objectives on the part of the individual scientists. In addition the occurrence of a larval phase in the life cycle of different phyla is probably due to convergent evolution, making a single definition very difficult, if not impossible. Smith (1977) defined larva as “An intermediate developmental form between eggs and adults”. His definition reflected a pragmatic approach to defining and identifying a sub population in the planktonic and benthic communities of the coastal marine environment. Hickman (1999) offers the definition: “The larva is a structural state or series of states that occurs between the onset of the divergent morphogenesis following embryonic development (cleavage, blastula gastrula) and metamorphosis to the adult”. This definition is independent of habitat, locomotion or function. Young (1999) included locomotion in his definition, “A larva is a postembryonic stage of the life cycle which differs from the adult morphologically and is capable of independent locomotion”. Davidson (1991) offers a definition emphasizing developmental factors: “A larva is the premetamorphic consequence of type I embryogenesis, a pattern of embryonic development characteristic of most invertebrates in which cell lineage plays an important role in the spatial organization of the early embryo. In this definition the invertebrate larva results from a type of specification of cell fates that

is fundamentally different until metamorphosis". Williamson (1992) offers an alternative interpretation proposing that the larva of many animal clades resulted from the hybridization of two different clades after the adult lineages of both clades had been established. This non - Darwinian mode of evolution, much like that of Sagan (1967) would define the larva as an extreme form of symbiosis. Each of these definitions has validity if taken in the context used by the respective researchers. The purpose of this work is to offer a key to identify those marine arthropod organisms, which have historically been labeled as larvae.

The Arthropoda, animals with segmented bodies, jointed appendages and exoskeletons composed of chitin represent the largest and most diverse phylum in the marine environment. Within the phylum Arthropoda there are two sub-phyla and eleven classes having larval stages in the marine environment. The subphylum Chelicerata, animals with a body divided into a prosomata and an opisthosomata and a single pair of appendages, chelicerae, anterior to the mouth. There are three classes in this sub-phylum: Pycnogonida, sea spiders; Arachnida, marine mites; and Merostomata, horseshoe crabs. The subphylum Crustacea, animals with five pairs of appendages on the head, including the classes Branchiopoda, Cephalocarida, Thecostraca: Facetotecta, Copepoda, Mystacocarida, Malacostraca, Ostracoda and the Remipedia. The scope of this key is restricted to the larvae of the above listed classes and four orders of copepods. The key is based on their morphology, patterns of body segmentation, numbers of appendages, and mode of locomotion.

Larvae may go through more than one distinct phase. In the case of Decapod Crustaceans three larval phases can be identified, nauplius, zoea and megalopa (Figs 1 & 2). In all of these larval phases, there may be one or more molts, up to five in the nauplii of the Copepoda, for example. The nauplius is the first postembryonic stage in mystacocaridans, cephalocaridans, branchiurians, copepods, euphausiids, remepedes, penaeide shrimp and thecostracans. The nauplius has three pairs of appendages, first and second antennae and mandibles, all of which are used for swimming in planktonic forms. These appendages may be modified for substrate attachment in benthic forms. Also they are used as sensory organs in the case of the first antennae and feeding in the case of the second antenna and mandibles. Of those crustaceans having a nauplius stage, arthrodival membranes separating somites are lacking in all groups except, branchiurians, cephalocaridans and mystacocaridans. A naupliar arthrite on the coxa of the second antenna is present in free-living copepod nauplii, thecostracans and cephalocaridans. The larvae of the Chelicerata, protonymphon larvae, hexapod larvae and the trilobite larvae may also go through more than one instar before metamorphosing into the adult body plan (Fig. 3).

Among some members of the Decapoda, the nauplius is followed by the zoea phase, which in turn is followed by the megalopa phase. Zoea defined as larvae having functional thoracic appendages that are used for swimming. Megalopa are defined as larvae in which the abdomen has functional swimming appendages. Some Crustaceans hatch as a Zoea. In the case of Isopods, the embryo develops in brood pouches into a developmental stage called the mancus, which are basically juveniles having one less pair of walking legs than the adults, and are never seen, in the marine environment (Kume and Dan, 1957).

An effort has been made to treat all traditionally named planktonic and benthic larval forms. In many cases larvae were collected from the plankton and described before their adult forms were known. In fact the Zoea were originally thought to be a marine arthropod and assigned the category of a genus, before J. V. Thompson discovered their true affinities in 1828 (see Young, 2002). Where feasible the original names of the various larval types have been used. Because this nomenclature is less commonly used today compared to the past, the more recent taxonomic affinities are included in parentheses after the original larval name.

2 Key to Marine Arthropod Larvae

- 1 (A) The larval body has arthrodival membranes.....2
- 1 (B) The larval body lacks arthrodival membranes.....4

- 2 (A) The thorax has swimming appendages. There are no abdominal swimming appendages. There are typically five pairs of appendages on the cephalosome.....9
- 2(B) The abdomen has swimming appendages. The thorax has swimming appendages. Typically five pairs of appendages are present on the cephalosome.....15
- 2 (C) Walking appendages are present on the thorax. One pair of chelicerae is present on the cephalosome.....3
- 2 (D) The first antennae are not segmented. The protopod of second antennae is more than half the length of the limb. The mandible uniramous.....Branchhiopoda Nauplii
- 2 (E) The first antennae are six segmented. The thorax and abdomen do not have appendages. Their habitat is interstitial water of muddy bottoms.....Cephalocarida Nauplii
- 2 (F) The first antennae are seven segmented. The thorax and abdomen do not have appendages. Found in interstitial water of sandy bottoms.....Mystacocarida Nauplii
- 3 (A) The abdomen is unsegmented with one pair of chelicera, four pair of walking appendages, which are chelate, and one pair of gill raking appendages. The larval body has a minimum of seven segments.....Trilobite Larva
(The larva of the Horseshoe Crab)
- 3 (B) The body of the larva is segmented with three pair of appendages on the head. The chelophores, first pair of cephalic appendages, are chelate. There is a proboscis on the head between the chelophores. There is one pair of derived appendages on each segment of the larval body posterior to the head. The appendages on the body segments may have many strong spines.....Later stages of protonymphon larvae
- 4 (A) There are three pairs of walking appendages on the larva's body.....Hexapod Larvae
(Larva of marine mites)
- 4 (B) There are three pairs of cephalic non-swimming appendages. The first pair of appendages are chelate.....Protonymphon
(The larva of the sea spiders, Pycnogonida)
- 4 (C) Three Pairs of un-derived cephalic swimming appendages are present.....Remipedia Nauplii
- 4 (D) Three pairs of derived cephalic swimming appendages are present.....5
- 5 (A) The cephalic shield is composed of platelets and a caudal spine. Frontal filaments are present in the form of tiny anlagenNauplius - Y Larvae
(Facetotecta)
- 5 (B) The cephalic shield composed of platelets is not present.....6
- 6 (A) The larvae have frontal filaments, horns and a caudal process with the furcal spines on the latter.....Cirripedia Nauplii
(Thecostraca)

- 6 (B) The larvae have frontal filaments and a caudal process with furcal spines on the latter, but no horns.....Ascothoracida Nauplii
(Thecostraca)
- 6 (C) Not as above, that is lacking frontal filaments.....7
- 7 (A) The larvae have a bivalve shell..... Ostracoda Nauplii
- 7 (B) The larvae have a telson and a rostral hood..... Euphausiacea Nauplii
- 7 (C) The larvae have a telson, but lack a rostral hood.....Penaeidea Nauplii
(Decapoda)
- 7 (D) Not as above.....8
- 8 (A) The body shape is ovoid. The first antennae are uniramous and three-segmented. The second antennae are biramous consisting of a two segmented protopod, a one segmented endopod and a five segmented exopod. The mandibles are biramous consisting of a two segmented protopod, a two segmented endopod and a four segmented exopod without gnathobase. The caudal armature is symmetrical.....Cyclopoida Nauplii
(Copepoda)
- 8 (B) The caudal armature is unequal. The body may be flexed ventrally in many taxa. The antennules and second antennae are held forward. The body is elongate in shape. The antennules are three segmented with a broad and elongate distal segment. The antennae are biramous consisting of a two segmented protopod, a two segmented endopod and a six segmented exopod. The mandible is biramous consisting of a two segmented protopod, a one segmented endopod and a four segmented exopod. The labrum is large and spinulose.....Calanoida Nauplii
(Copepoda)
- 8 (C) The antennules are held perpendicular to the long axis of the body. The body shape is broad and more or less discoid. The antennules are three segmented. The second antennae are biramous consisting of a two-segmented protopod, and a one segmented endopod. The mandible has a long terminal seta on the exopodite. The mandibular endopodite has one or two stout setae on the inner process terminally.....Harpacticoida Nauplii
(Copepoda)
- 8 (D) The antennules have more than three segments. In *Canuella* there are five segments in the NI – NVI stages. In *Longipedia*, there are six segments in the NI stage and five segments in NII - NVI. The body shape is broad and more or less discoid. The members of the genus *Longipedia* have a long pointed structure resembling a spine on the posterior of the body. This makes this genus resemble the nauplii of Cirripedia. They can be distinguished from the latter by the presence of the furcal spines on the ventral side of the body at the base of the spine-like structure. The second antennae are biramous consisting of a two-segmented protopod and a coxa with a six-segmented exopod becoming nine-segmented in the NVI stage.....Polyarthra Nauplii
(Copepoda)
- 9 (A) The cephalosome is covered by a bivalve shell. Sessile compound eyes are present. Six pairs of derived thoracic appendages are present. This is a non-feeding larval stage, which follows the NVI Nauplius stage in barnacles. This is the larval stage in which the animal settles on a suitable substrate..... Cypris Larva of the Cirripedia

- 9 (B) The larva has a large spherical carapace covering the cephalothorax, up to six (6) centimeters in diameter. They swim by the thoracopods. Pleopods are not present on the larvae.Eryonecius (family Polychelidae lobster)
- 9 (C) The body of the larva is shrimp-like in form.....10
- 9 (D) The body of the larva is strongly compressed and transparent.....12
- 9 (E) The body of the larva has strong dorsal and/or rostral spines..... 13
- 9 (F) The segmented larval body consists of a head, a segmented thorax and a segmented abdomen. A many faceted head shield covers the head and anterior portion of the thorax. The head shield is free from the thorax. The nauplius eye is dorsal to the two large compound eyes on the head shield. The labrum and antennules are on the ventral side of the head below the compound eyes. There is a pair of biramous thoracopods on each thoracic segment. The abdomen terminates in a telson with a pair of furcal spines.....Cypris-Y Larva (Facetotecta)
- 10 (A) The larva lacks maxillipeds.....14
- 10 (B) The anterior most thoracopods are modified as maxillipeds.....11
- 11 (A) The larvae have compound eyes, sessile in the first stage and stalked in the second and third stages. The telson is divided. The antennal exopod is segmented. More than 1, but less than 8 pair of thoracopods is present. The uropods are not setose.....Elaphocaris Larvae (Protozoa of the Dendrobranchiata)
- 11 (B) Compound eyes are present, usually un-stalked in early stages and stalked in later stages. There are eight pairs of thoracopods present from the first stage, the first three modified as maxillipeds and the fourth pair being chelate from stage I. A rostral spine is present from the first stage on. The abdominal segments lack pleopods, but have dorsal and lateral spines on segment 1 to 5. With each molt the fourth pair of thoracopods becomes larger than the last four. The exopodites of the last five pair of thoracopods are greatly reduced in the first stage and disappear by the fifth stage..... Mysis Larvae (Homaris americanus)
- 11 (C) Shrimp-like larvae lacking spines over the sessile compound eyes. The posterior lateral spines are parallel to the long axis of the body of the larval body. The carapace is one-third of the total length of the body. The sixth abdominal segment is armed with a spine directed toward the posterior. The telson is slightly notched.....Lucifer Zoa
- 11 (D) The larvae are shrimp-like and have simple spines over the compound eyes. The compound eyes are on short stalks. The posterior lateral spines are oblique to the long anterior- posterior axis of the body and project slightly beyond the outline of the carapace. The carapace is about one-half the length of the body. All abdominal segments are armed with posteriorly directed spines. The telson is deeply notched.Acetes Zoa
- 11 (E) The larvae are shrimp-like having long branched spines over the compound eyes. The compound eyes are on very long stalks in later stages. In early stages the antennal exopod may be unsegmented. The posterior lateral spines are perpendicular to the long axis of the body. The carapace is more than two-thirds of the body

length. All abdominal segments are armed with spines more or less perpendicular to the long axis of the body. The branches of the telson extend perpendicular to the long axis of the body..... Acanthosoma larva (Sergestes Zoea - See Larva of Decapoda: Crustacea By R. Gurney 1936 for a key to species)

12 The antennal exopod is unsegmented. Compound eyes are present, usually un-stalked in early stages and stalked in later stages. The body is strongly compressed. More than one pair of functional thoracopods is present. In later stages all thoracopods may be present and pleopod buds may be present.....Phyllosoma (Palinura)

13 (A) The cephalon and thorax are covered by a carapace, which is not attached to the thorax. The carapace has a prominent rostral spine and two posterior pointing spines. There are five pairs of derived appendages on the thorax. The eyes are stalked.....Antizoea Larva (Stomtopoda)

13 (B) The larva have all five pairs of cephalic appendages and sessile eyes plus two or three pairs of maxillipeds, at the time of hatching. The carapace is oval in shape and the larva has well developed rostral spines, one directed anteriorly parallel to the axis of the larval body and a second shorter spine directed posteriorly from the carapace margin.....Anomuran Zoea

13 (C) At the time of hatching the larva has all five pairs of cephalic appendages and sessile eyes and two pairs of maxillipeds are present. The abdomen is unsegmented in the first zoeal stage. In latter stages the larvae have well developed rostral spines one directed anteriorly and ventrally and a second shorter spine curved in the posterior direction from a dorsal position on the carapace. A third maxilliped is present and the abdomen becomes segmented..... Brachyuran Zoea

14 (A) Sessile compound eyes are present beneath the carapace in all three stages. One pair of functional thoracopods is present. The telson is undivided. The antennal exopod is segmented. The uropods are setose in the third stage.....Calyptopis Larvae (Euphausiacea)

14 (B) The eyes are movable and not covered by the carapace. The animal uses both the antennae and thoracic appendages to swim. The three-segmented peduncle of the antennules is much longer than the antennal exopod. The telson remains undivided. All of the pleopods are present and the second to eighth pair of thoracopods appear as buds.....Furcilia Larva (Euphausiacea)

15 (A) The larva lacks maxillipeds.....16

15 (B) The larva has maxillipeds.....17

16 The larva has the appearance of a shrimp, but with eight pair of biramous thoracopods none of which is modified as maxillipeds. The gills are attached to the base of the thoracopods and protrude beyond the margin of the carapace.....Crytopia Larva (The equivalent to a megalopa stage in the Euphausids)

17 (A) The larva is transparent.....18

17 (B) The larva is not transparent.....19

18 Flattened transparent body resembling the adult form of a Scyllaride adult with well-developed pleopods, five pair of functional thoracopods. The antennules are present as flattened plates or elongated structures.....Puerulus Larva (Palinura)

19 (A) The cephalon and thorax are covered by a carapace, which is not attached to the thorax. The carapace has a prominent rostral spine and two posterior pointing spines. There are five pairs of derived appendages on the thorax and fully developed pleopods on the abdomen. A pair of raptorial appendages are present.....Alima Larva (Stomatopoda)

19 (B) The larva has a more or less oval cephalothorax (less than twice as long as wide). The first pair of thoracopods is chelate and the last four thoracopods modified as walking legs. All Thoracopods are uniramous in this stage. The abdominal pleopods are uniramousMegalopa Larva (Brachyuran crab larva)

19 (C) The larva has an elongated cephalothorax (at least twice as long as wide), with a pair of strongly chelated thoracopods plus four thoracopods modified as walking legs. All thoracopods are uniramous in this stage. The abdominal appendages are biramous.....Glaucothoe (Megalopa of an anomuran)

19 (D) The larvae have a large spherical carapace covering the cephalothorax, up to six centimeters in diameter. They swim by their thoracopods and well-developed abdominal pleopods. The male reproductive structures may be present in older larvae..... Eryonecius (family Polychelidae lobster)

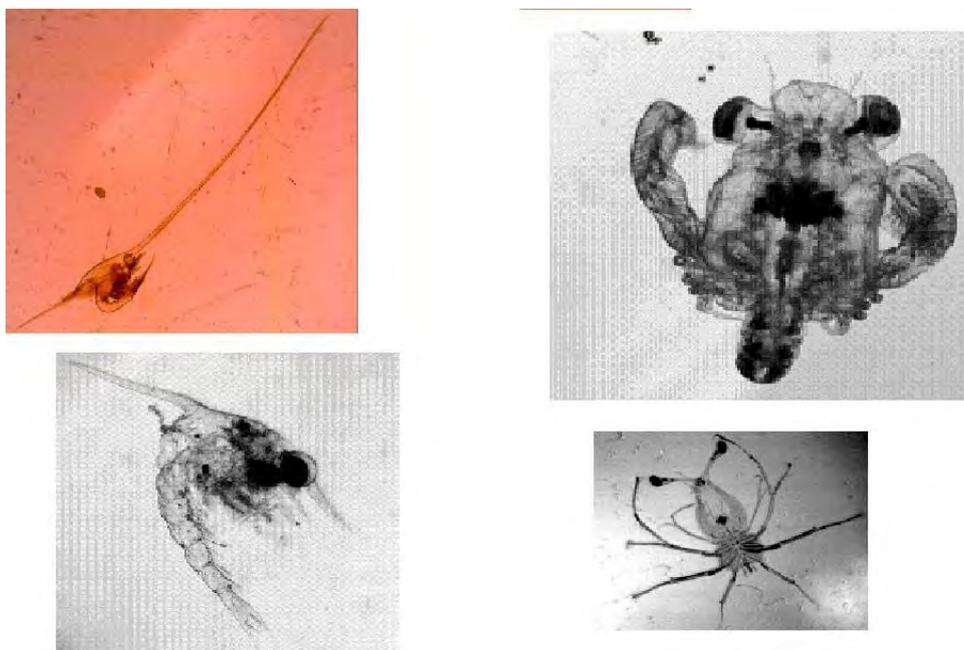


Fig. 1 Anomuran zoea in the upper left, brachyuran megalopa in the upper right, brachyuran zoea in the lower left and phyllosoma larva in the lower right.

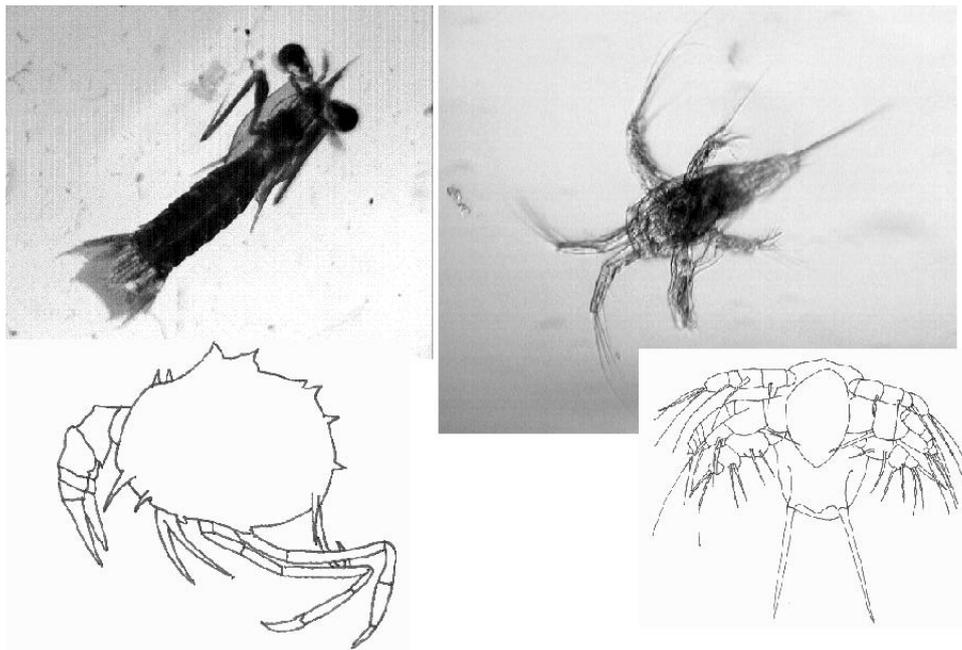


Fig. 2 Alima larva of a Stomatopod in the upper left, calanoid nauplius in the upper right, eryonecius larva in the lower left and a Polyarthra nauplius larva in the lower right (After Dahms, 2000).

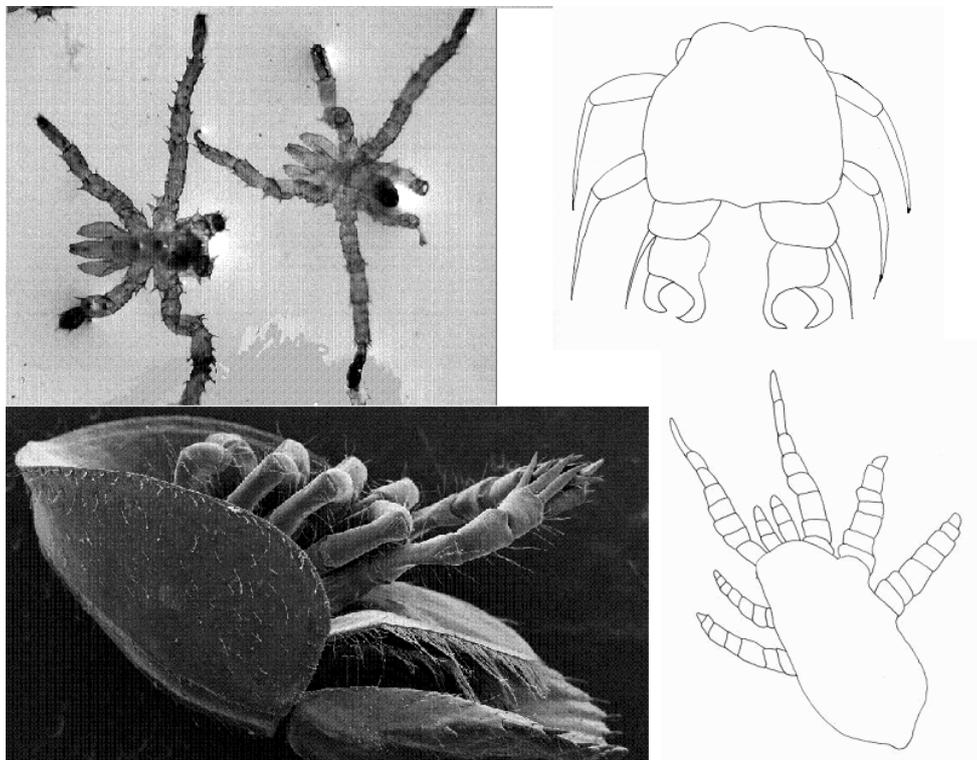


Fig. 3 The juvenile stage of *Ammothea glacialis* is in the upper left, trilobite larva of *Limulus polyphemus* is in the lower left. Protonymphon larva is in the upper right (After Brusca, 1975). Hexapod larva in the lower right and (After Pugh, 1996).

3 Glossary

Abdomen: The third segment, posterior segment of the body.

Antennule: The anterior most appendages on the head of members of the subphylum Crustacea.

Class Arachnida: Chelicerates with typically four pair of walking legs, a waxy cuticle, with tracheae and book lungs for respiration.

Class Branchiopoda: Small crustaceans found mostly in fresh water. The trunk appendages have a flattened leaf-like structure. Members of the Branchiopoda are also characterized by the presence of gills on many of the animal's appendages.

Class Cephalocarida: Small crustaceans, which have elongated segmented bodies. The first eight segments of the body posterior to the head bear biramous appendages.

Class Cirripedia: Sessile thecostracans, which have the body enclosed in a bivalved carapace. The carapace is not hinged as in the Ostracoda. The First and Second antennae are reduced or may be absent. These animals may be free-living or parasitic.

Class Copepoda: Small crustaceans, typically with cylindrical bodies. They have five pair of biramous appendages on the thorax, which are fused together by an intercostals sclerite.

Class Malacostraca: Crustaceans having a trunk composed of fourteen segments all of which bear appendages. The thorax is composed of the first eight segments and the abdomen the last six. The gonopores of the females open ventrally on the fifth thoracic segment. The gonopores of the males open ventrally on the eighth thoracic segment.

Most of the species in this class have compound eyes.

Class Merostomata: Marine chelicerates having five or six pairs of abdominal appendages modified as gills. A spike-like telson is also present.

Class Mystacocarida: Marine crustaceans found in interstitial fluid with elongated cylindrical bodies. The first five segments on the body bear appendages.

Class Ostracoda: Marine crustaceans with a hinged bivalve carapace. The trunk of the body is reduced and has no more than two pair of appendages.

Class Pycnogonida: Benthic marine chelicerates with typically four pair of nine segmented walking legs. The mouth is located at the end of a cylindrical proboscis, which may be nearly as long as the rest of the animal. There are four eyes on a tubercle on the dorsal side of the head.

Class Remipedia: Crustaceans with elongated segmented bodies resembling polychaete worms. Each segment has a pair of biramous appendages.

First Antennae: The anterior most appendages on the head of members of the subphylum Crustacea. Also called an antennule.

Frontal filaments: A pair of elongate sensory organs located on the ventral side of the nauplius and cypris larvae of the Thecostraca.

Head: The anterior most segment of the body. The mouth, sensory appendages and feeding appendages are usually present.

Larval Phase: A term used to describe different stages of larval development in animals such as the nauplius, calyptopis and furcilia larva of the Euphausiacea. Each is said to be a stage in the larval phase of development.

Maxilliped: The first one to three thoracic appendages, modified for feeding.

Pleopod: an abdominal appendage, which may be used for swimming.

Rostrum: A dorsal plate covering the cephalothorax in members of the Malacostraca.

Rostral Hood: An anterior extension of the dorsal carapace in the larva of euphausiids.

Second Antenna: Biramous sensory appendages, posterior to the first antennae.

Subphylum Chelicerata: Animals with a body divided into a cephalothorax and an abdomen and a single pair of appendages, chelicerae, anterior to the mouth, Subphylum Crustacea, animals with five pairs of

appendages on the head.

Telson: The unpaired terminal segment of members of the Crustacea.

Thoracopod: Any thoracic appendage of the Malacostraca.

Thorax: The second or middle body segment in arthropods.

Type I Embryogenesis: a general developmental pattern characteristic of most invertebrate taxa, in which lineage plays an important role in the spatial organization of the early embryo, and cell specification occurs *in situ*, by both autonomous and conditional mechanisms.

Un-derived: A term used to describe appendages, which lack arthrodistal membranes between segments.

Uropod: The sixth abdominal appendages of malacostracans.

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References

- Belmonte G. 2005. Y-nauplii (Crustacea, Thecostraca) from the coastal waters of the Salento Peninsula (Southeastern Italy, Mediterranean Sea) with descriptions of four new species. *Marine Biology Research*, A (4): 254-256
- Bjornberg TKS. 1965. Observations on the Development and the Biology of the *Miracidia dana* (Copepoda, Crustacea). *Bulletin of Marine Science*. 15(2): 512-520
- Bjornberg TKS. 1967. The larvae and young forms of *Eucalanus dana* (Copepoda) from tropical Atlantic waters. *Crustaceana*, 12(1): 59-73
- Bjornberg TKS. 1972. Developmental stages of some tropical and subtropical planktonic marine copepods. *Studies on the Fauna of Curacao and Other Caribbean Islands*, 40: 1-185
- Bjornberg TKS. 1998. Description of Canuellid Nauplii of Sao Sebastiao Channel (Southeastern Brazil) Nauplius, Rio Grande, 6: 155-160
- Bjornberg TKS, Lopes RM, Bjornberg HGC. 1994. Chave Para A Identificacao De Nauplios De Copepodos Planctonicos Marinhos Do Atlantico Sul- Ocidental. *Nauplius*, Rio Grande, 2: 1-16
- Brusca GJ. 1975. *General Patterns of Invertebrate Development*. 134, Mad River Press
- Charmantier G, Aiken DE. 1987. Intermediate larval and post larval stages of *Homarus americanus* H. Milne Edwards, 1837 (Crustacea: Decapoda). *Journal of Crustacean Biology*, 7(3): 525-535
- Dahms HU. 1990. Naupliar development of Harpacticoida (Crustacea, Copepoda) and its significance for phylogenetic systematics. *Microfauna Marina*, 6: 169-272
- Dahms HU. 2003. A Pictorial key for the identification of crustacean nauplii from the marine meiobenthos. *Journal of Crustacean Biology*, 13(3): 609-616
- Dahms HU. 1996. *The Crustacean Nauplius - a Reappraisal*. Habilitationsschrift zur Erlangung der venia legendi des Fachbereichs Biologie der Universitat Oldenburg. 114
- Dahms HU. 2000. Phylogenetic implications of the Crustacean nauplius: Advances in copepod taxonomy. *Hydrobiologia*, 41: 91-99
- Dahms HU. 2004a. Exclusion of the Polyarthra from the Harpacticoida and its reallocation as an underived branch of the Copepoda (Arthropoda, Crustacea). *Invertebrate Zoology*, 1(1): 29-51
- Dahms HU. 2004b. Postembryonic apomorphies proving the monophyletic status of the Copepoda. *Zoological Studies*. 43(2): 446-453
- Dahms HU, Fornshell JA, Fornshell BJ. 2006. Key for the identification of crustacean nauplii. *Organisms Diversity and Evolution*, 6(1): 47-56

- Davidson EH. 1991. Spatial regulation of gene expression in metazoan embryos. *Development*, 113: 1-26
- Fanta ES. 1972. Anatomy of the nauplii of *Euterpina acutifrons* (Dana) (Copepoda, Harpacticoida) *Crustaceana*, 23(2): 167-181
- Fanta ES. 1976. Anatomy of the nauplii of *Oithona hebes* Herbst (Copepoda, Cyclopoda). *Bolm. Zool. Univ. S. Paulo*, 1: 205-238
- Felder DL, Martin JW, Goy JH. 1985. Patterns in Early Postlarval Development of Decapods in Larval Growth (Wenner AM, Balkema AA, eds). 163-225, Boston, USA
- Ferrari FD, Ambler JW. 1992. Nauplii and copepodids of the cyclopoid copepod *Dioithona oculata* (Farran, 1913) (Oithonidae) from a mangrove cay in Belize. *Proceedings of the Biological Society of Washington*. 105(2): 275- 298
- Fornshell JA. 1994. Copepod nauplii from the barrier reef of Belize. *Hydrobiologia*, 292/293: 295-301
- Green J. 1974. Crustaceans. In: *Experimental Embryology of Marine and Fresh-water Invertebrates* (Reverberi G, ed). 312-361, North-Holland Publishing Company, London, UK
- Gurney R. 1930. The larval stages of the copepod Longipedia. *Journal of the Marine Biology Association*, 16: 461-474
- Gurney R. 1942. *Larvae of Decapod Crustacea*. Ray Society, London, UK
- Haq SM. 1965 Development of the copepod *Euterpina acutifrons* with special reference dimorphism in the male. *Proceedings of the Zoological Society of London*, 144(2): 175-201
- Hickman CS. 1999. Larvae in invertebrate development and evolution. In: *The Origin and Evolution of Larval Forms* (Hall BK, Wake MH, eds). 423, Academic Press, London, UK
- Itoh T. 1989. A new species of *Hansenocaris* (Crustacea: Facetotecta) from Tanabe Bay, Japan. *Publications of the Seto Marine Biology Laboratory*, 34(1/3): 55-72
- Itoh H, Nishida S. 1997. Naupliar stages of *Hemicyclops japonicus* (Copepoda: Poecilostomatoida) reared in the laboratory. *Journals of Crustacean Biology*, 17: 162-173
- Izawa K. 1987. Studies on phylogenetic implications of ontogenetic features in Ptheoecilostome nauplii (Copepoda: Cyclopoda). *Publications of Seto Marine Biology Laboratory*, 32(4/5): 151-217
- Kikuchi T, Kazutaka T, Sigeo G. 1991. Nauplius – Y (Crustacea: Maxillopoda: Facetotecta) from Manazuru, Sagami Bay, Central Japan.
- Knight MD. 1973. The nauplius II Metanauplius and Calyptopis stages of *Thysanopoda tricuspidata* Milne-Edwards (Euphausiacea). *Fisheries Bulletin*, 71: 53 –67
- Koenemann S, Schram FR, Bloechi A, et al. 2007 Post-embryonic development of remipede crustaceans. *Evolution and Development*, 9(2): 117-121
- Kume M, Dan K. 1957. *Invertebrate Embryology*. Bai Fu Kan Press, Tokyo, Japan
- Lovegrove T. 1956. Copepod Nauplii (II) Conseil International Pour L'Exploration De La Mer. (Zooplankton Sheet 63)
- Manning RB. 1962. Alima Hyalina Leach, the pelagic larva of the stomatopod crustacean *Squilla alba* Bigelow. *Bulletin Marine Science of the Gulf and Caribbean*, 12(3): 496-507
- Martin J W, Truesdale FM, Felder DL. 1988. The megalopa stage of the Gulf Stone crab, *Menippe adina* Williams and Felder 1986 with comparison of Megalopae in the genus *Menippe*. *Fishery Bulletin*, 86(2): 289-297
- Mauchline J. 1971. Euphausiacea larvae Conseil International Pour 'Exploration De La Mer (Zooplankton Sheets 135/137)
- McEdward L. 1995. *Marine Invertebrate Larvae*. CRC Press Washington DC, USA
- McLaughlin PA. 1980. *Comparative Morphology of Recent Crustacea*. W.H. Freeman and Co., San Francisco, USA

- McLaughlin PA, Lemaitre R, Tudge C. 2004. Carcinization in the Anomura – fact or fiction? II Evidence from larval, megalopal and early juvenile morphology. *Contributions to Zoology*, 73(3) (<http://dpc.uba.uva.nl/ctz/vol73/nr03/art01>)
- Nicholls AG. 1935. The larval stages of *Longipedia coronata* Claus, *L. scotti* G. O. Sars, and *L. minor* T. and *A. Scott*, with a description of the male of *L. scotti*. *Journal of the Marine Biology Association*, 20(1): 29- 46
- Ogilvie H. 1953. Copepod Nauplii (I) Conseil International Pour 'Exploration De La Mer (Zooplankton Sheet 50)
- Onbe T. 1984. The developmental stages of *Longipedia americana* (Copepoda: Harpacticoida) reared in the laboratory. *Journal of Crustacean Biology*, 4(4): 615-631
- Pechenik JA. 1991. *Biology of the Invertebrates* Second edition. Wm. C. Brown Publishers, Iowa, USA
- Pugh PJA. 1996 The Structure and function of the tarsus I sensillar field in mites of the genus *Halarachne* (Halarachnidae: Gamsida). *Journal of Natural History*, 30(7): 1069-1086
- Reports of the Manazuru Marine Laboratory for Science Education. Faculty of Education, Yokohama National University, 7: 65-75
- Roberts P B. 1968. A giant scyllarid Phyllosoma larva from the Caribbean Sea, with notes on smaller specimens (Palinuridae). *Crustaceana*, Supplement 2: 83-97
- Rodrigues SI, Manning RB. 1992. The first stage larva of *Coronis scolopendra* Latreille (Stomatopoda: Nannosquillidae). *Journal of Crustacean Biology*, 12: 79-82
- Ruppert EE, Barnes RD. 1994. *Invertebrate Zoology* (6th Edition). Saunders College Publishing, Philadelphia, USA
- Sagan L. 1967. On the origin of mitosing cells. *Journal of Theoretical Biology*, 14(3): 255-274
- Smith DL. 1977. *A Guide to Marine Coastal Plankton and Invertebrate Larvae*. Kendall/Hunt Publishing Company
- Squires, H. J. 1996 Larvae of the hermit crab, *Pagurus arcturus* from plankton (Crustacea, Decapoda). *Journal of Northwest Atlantic Fisheries Science*, 18:43-56
- Subramanyan CB. 1971 Description of shrimp larvae (Famils penaeidae) off the Mississippi coast. *Gulf Research Reports*, 3: 241-258
- Williamson DI. 1983. *Crustacean Decapoda: Larvae Fiche No. 167/168*. Council International Pour L'Exploration De La Mer. 8
- Williamson DI. 1992. *Larval Evolution: Towards a New Zoology*. Chapman and Hall, New York, USA
- Young C. 1999. Marine invertebrate larvae. In: *Encyclopedia of Reproduction* (Knobil E, Neil JD, eds). 89-97, Academic Press, London, UK
- Young C, Rice M. 2002 *Atlas of Marine Invertebrate Larvae*. Academic Press, USA